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Bottleneck Tubers and Jelly-End Rot In the Russet Burbank Potato

L. W. Nielsen and W. C. Sparks[1]

The Russet Burbank variety of potatoes may produce numerous malformed tubers having little commercial value. The malformed tubers arise from what is known as "second growth" and may assume one of two general types. One type consists of secondary lateral growth originating at the "eyes" of the tuber and producing what are known locally as knobby potatoes. The second type of tuber malformation consists of secondary longitudinal growth resulting in potatoes known as bottlenecks, dumbbells, and other forms. Tubers affected with secondary longitudinal growth must be utilized for preparing lower commercial grades (U. S. Standard or U. S. No. 2) or cullage. Culls are frequently used as stock feed or for processing various industrial products. The ultimate use of a malformed potato will depend on its size and the severity of the malformation. The monetary loss to the grower may be as much as 75 percent of the crop value. In addition, jelly-end rot at harvest or in early storage is frequently associated with tubers exhibiting symptoms of secondary longitudinal growth.

Both types of second growth have been attributed to alternate periods of drouth and adequate moisture during plant growth —particularly in late summer. For years numerous Idaho potato growers have meticulously followed irrigation schedules designed to maintain uniform soil moisture throughout the potato-growing season, but still malformed potatoes of both types comprise one of the major sources of cullage or low grade potatoes. Kraus reported that plant population influenced the production of knobby potatoes to a greater extent than faulty irrigation (6).[2] This paper summarizes the results from experiments studying the effect of various factors on the production of bottle-neck and related tuber types, and the results from preliminary studies on the relationship between bottle-neck potatoes and jelly-end rot.

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[2] Figures in parentheses refer to literature cited.

Review of Literature

Abnormal elongation of potato tubers during development is generally referred to as second growth. This defect has been associated with drouthy soil conditions during tuber enlargement for many years (5). High temperatures during tuber formation and growth are reported to reduce yields and modify tuber shape, and that the deleterious effects will be more pronounced if the high temperatures are accompanied with drouth (1,17). The cause of secondary tuber elongation is based upon observational data but most reports agree that drouth is the predisposing factor (3, 10, 12, 14, 17). Various proportions of N- P- K in commercial fertilizer formulations are reported to influence tuber shape (4, 7).

Variously shaped tubers are produced by the secondary growth or elongation of the longitudinal axis. Round (1, 12) and long (10) tuber varieties are susceptible to secondary growth. The tuber form most frequently illustrated or described has a stem-end smaller in diameter than the bud-end (4, 9, 10, 12, 14) and referred to as "bottleneck" (10). A second tuber form frequently illustrated has a constriction along the longitudinal axis leaving a bulb of tissue at both the stem- and bud-ends of the tuber (1, 10, 14). This tuber form has been called the "dumbbell" (1). The affected tubers may also be curved from the normal axis of growth (14).

The stem-ends of potatoes affected with second growth sometimes wither or shrivel. The shriveled condition is sometimes evident at harvest (9, 10), or it may develop in storage (1). In many cases when a withered second growth tuber is cut in half longitudinally, the internal tissue of the withered stem-end appears to be water-soaked in contrast to the white appearance of tissue at the distal end. This water soaked or translucent tissue has been described as "glassy" (3, 10, 12, 14).

The glassy appearance is due to the absence of starch grains in the cells. This can be demonstrated microscopically (3, 12), by the iodine-potassium iodide starch test (12, 14), or by specific gravity (10, 12). In contrast to normal starchy tissue, chemical analyses show that the glassy tissue is low in solids and starch and rich in sugars (12).

Second growth tubers with the glassy end are more susceptible to decay (12, 14). Decay is found most often in long tuber varieties (10) and is called jelly-end rot. Jelly-end rot has been a production and storage problem of the Burbank and Russet Burbank varieties in western United States for many years (2, 8, 11, 16). It has been pointed out that in these western grown varieties jelly-end rot occurs usually at the abnormal stem-ends (8, 15) and illustrations in various papers clearly show that stem-ends of bottleneck tubers are involved (2, 9, 13). Jelly-end rot

has been reported to develop occasionally in knobs (15) and in the bud-end (13, 15).

The rotted potato tissue is very soft (8) and may be easily broken or sloughed from the affected tuber (10). It is a wet rot and "at first nearly white, turning yellow then light brown and finally dark brown" (15). In storage the water evaporates leaving only the collapsed "skin" attached to the stem-end (2). The glassy tissue and the jelly-like rot that may displace it have been likened to the starch-free tissue and the rot that frequently develop in potato seedpieces that have produced potato plants (15).

It is generally agreed that jelly-end rot is limited to the stem-end and seldom destroys over 2 inches of tissue (8, 10, 15). However, it is reported that the entire tuber may be destroyed (2). The affected tissue is sharply delimited from sound tissue (9, 10, 15). The amount of tuber destroyed by the rot appears to vary with the potato affected (9, 15) and related to "the extent of abnormal elongation of the stem-end" (15).

The etiology of jelly-end rot is not clearly understood. Various potato fungal pathogens and numerous saprophytic fungi and bacteria have been isolated from diseased tubers, but no organism has been convincingly demonstrated as the casual agent. The wilt pathogens *Verticillium albo atrum* and *Fusarium oxysporum* were believed to form the "means of entrance for other fungus and bacterial diseases of the tubers such as jelly-end and dry rot" (16). Orton considered jelly-end rot an early form of dry-end rot associated with *Fusarium oxysporum* (11). On the basis of isolation and inoculation studies Carpenter reported that jelly-end rot was associated with *F. oxysporum* and *F. radicicola* with the latter being most important (2). Pratt also reported *F. radicicola* capable of causing a jelly-end rot similar to that found in nature, but wrote that, in the field—"some adverse condition, however, is probably responsible for its development" (13). *Rhizoctonia solani* was the only pathogenic organism isolated by Shapovalov from tubers having jelly-end rot. He inoculated 5 elongated tubers at the stem-ends and on the side. They were incubated 17 days in sterile moist sand and a jelly-like rot developed at the stem-ends. That rot which developed at the side inoculations was soft but not jelly-like. He reported that *R. solani* was an important causative agent of jelly rot in elongated tubers, but postulated that "the jelly-like consistency is determined more by certain abnormalities of the host tissue (low starch) than by species of the parasite" (15).

Schlumberger found bacteria associated with jelly rot (14). After isolating a number of pathogenic and numerous miscellaneous fungi, McKay postulated "that the appearance of the trouble depends more on climatic conditions than it does on the presence of any one or two or three organisms" (8). Murphy found no pathogenic organisms present in the jelly-end rot (10).

Materials and Methods

The Russet Burbank variety was used for all experiments, and planted according to prevailing commercial practices. Cut seed pieces averaging 1½ to 2 ounces in weight were planted with mechanical planters or by hand about 12 inches apart in rows 36 inches wide. To assure adequate soil moisture for plant emergence and early growth the land was usually irrigated several days before preparing the seed bed. The seedpieces were planted about 2½ to 3 inches deep and the crop was first cultivated when the emerging plants made the row visible. Subsequent cultivations, or the preparation of water furrows were made according to the need for weed control or irrigation. As the growing plants approached the height of approximately 10 to 12 inches, or when the vines from adjoining rows approached contact the final cultivation and ridging of the rows was made. For a number of experiments portions of fields planted to commercial table stock production were used as plots.

Randomized blocks were used in most experiments and a minimum of 4 replications was used in field experiments. The plot size varied with the different experiments. In those experiments studying the effect of date of planting each plot consisted of a single row, whereas for those studying the effect of time of first irrigation each plot was three or four rows wide and the data are based upon the center one or two rows. The harvested plots were either 40 or 45 feet in length.

All data from replicated plot experiments were analyzed by the analysis of variance and appropriate tests of significance computed. Correlation coefficients (r) were calculated for some paired data.

Figure 1. Russet Burbank tubers selected to illustrate various forms that have resulted from secondary growth along the longitudinal axis. From left to right: normal conformation, bottleneck, dumbbell, twisted, pointed-bud-end. Stem-end in each case at top.

Figure 2. Two bottleneck tubers after about 1 month storage showing the shrivelled symptom of the affected stem-end (tuber at left) in contrast to a bottleneck tuber that remained firm.

Tuber Symptoms

The malformed tubers most generally recognized by the growers and sorting crews are those known as bottlenecks and dumbbells (Fig. 1). Tubers with the bottleneck symptoms have a smaller diameter at the stem-end than at the distal- or bud-end. The stem-end diameter may be only slightly smaller, or it may be less than ½ inch in diameter, while the distal portion resembles a normal tuber. The reduced stem-end diameter may extend for less than ½ inch along the longitudinal axis or it may exceed more than one-half the length of the tuber. Frequently, the bottleneck tuber is curved from the normal axis of growth. The curvature is most noticeable at the juncture of the smaller stem-end and the bulbous distal-end. Badly curved tubers may define a half circle. After several weeks in storage bottleneck tubers are frequently shrivelled and soft at the stem-end (Fig. 2).

The typical dumbbell tuber of Figure 1 has a pronounced constriction approximately at the middle of the longitudinal axis with the stem- and distal-ends bulbous and about equal size. The constriction may be very short, holding the bulbous ends appressed tightly together; or the constriction may be an inch or more in length, holding the bulbous ends some distance apart. The diameter of the constriction varies widely from only slightly less than that of the bulbous ends to a fraction of an inch in diameter. As with the bottleneck tuber the dumbbell tuber is frequently curved. Tubers classified as dumbbells may deviate considerably from the typical, but in general tubers were so classified if the diameters of both ends were greater than that of the constriction. A few dumbbell tubers were found shrivelled at the stem-end after being in storage.

The twisted and pointed-bud-end tubers in Figure 1 were types arbitrarily differentiated for this study. The twisted tubers were more or less uniform in diameter but curved from a straight longitudinal line of growth. Some of these also shrivelled at the stem-end in storage. Tubers of the pointed-bud-end type had normal conformation for the variety but had a nipple-like growth from the distal rosette of buds. This terminal growth deviated in form from that resembling the point of a pencil to

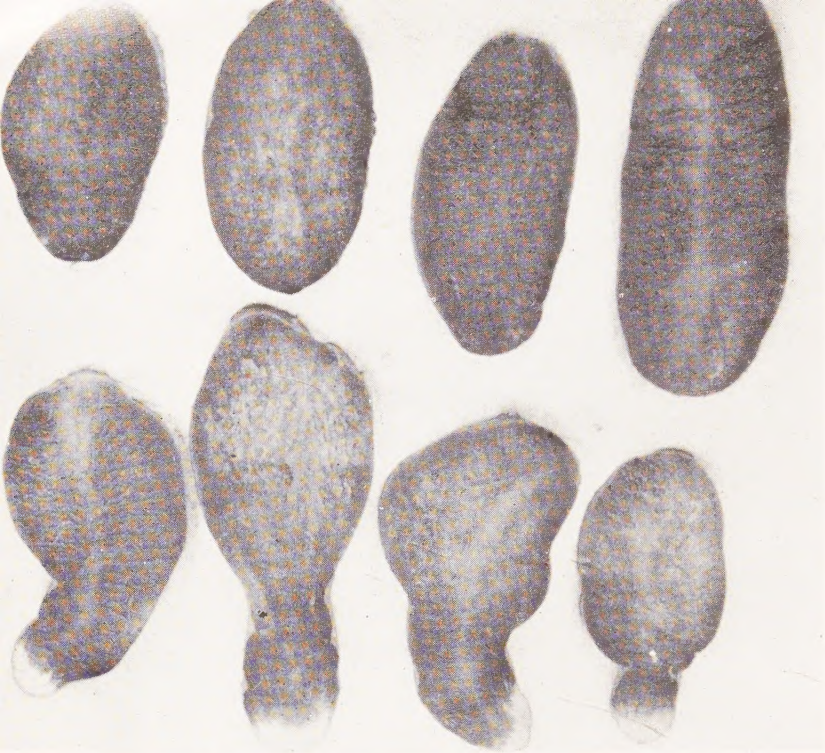

Figure 3. Median longitudinal slices from normal (top) and bottleneck (bottom) tubers after staining in an iodine - potassium iodide solution. In both sets of slices the stem-end is toward the bottom of the picture. The starch free area at the stem-end of bottleneck tubers did not stain blue.

the bulbous growth illustrated. No pointed-bud-end tubers were found with shrivelled stem-ends.

A median longitudinal section through a bottleneck tuber, particularly one with the shrivelling symptom, reveals a glassy, hydrotic, internal tissue at the stem-end. The tissue is devoid of starch and resembles in color and texture the internal tissue of an exhausted seed piece. The glassy, hydrotic tissue may be confined to a limited area near the stolon connection and has been observed to extend down a bottleneck nearly 1 inch. The starch-free area gradually blends into the normally white, starch-filled storage tissue.

That the glassy tissue is devoid of starch can be demonstrated by immersing longitudinal slices in an I-KI solution (Fig. 3). In normal potatoes the starch is present through the tuber; in the affected tuber it is virtually absent for various distances from the stem-end. The iodine-starch test also shows the transition from starch-free to starch-filled tissue. In some cases the transition region is fairly short, 1 to 2 millimeters. Starch-free stem-ends were frequently observed in twisted tubers, occasionally in dumbbell tubers, but not in pointed-bud-end tubers.

The four types of tuber malformation described and illustrated above were not recognized when the first observations of this work were made in 1945. The populations of bottleneck and dumbbell forms were studied in the earlier experiments. As time progressed the twisted and pointed-bud-end forms were included. The four malformed types were not always readily separable. In an affected crop of potatoes it is often possible to

select malformed tubers to illustrate a transition from one type to another, and it was frequently necessary to place arbitrarily a transition tuber in the form it most closely resembled. Usually one or two of the forms predominate in a malformed crop of potatoes. This arbitrary classification of tuber forms has proved helpful in demonstrating their relationship. In several of the tables to follow, the data would be much more impressive and significant if the several forms were grouped together as "malformed tubers".

Experimental Studies

That bottleneck tubers might be associated with drouth during tuber growth was first observed in 1945. In an experiment designed to test the effect of drouth on the production of knobby potatoes it was observed that plants deprived of irrigation water when the tubers were about one-fourth developed (July 19 to August 14) produced mature tubers that tended to have stem-ends smaller in diameter than plants not subject to drouth, or those deprived of water at a later stage of tuber growth. This suggested that a drouth period early in tuber development might induce the production of bottleneck tubers.

Under arid western conditions drouth during early tuber growth can be accomplished by two procedures. First, the initial irrigation can be delayed; second, the planting date can be varied and irrigation practices held constant. This latter procedure would most closely simulate natural conditions as the planting date is usually governed by the earliness of favorable spring weather, but potato irrigation begins about the first week of July. The slope of the land may also influence the water content of surface irrigated soil. Land having a relatively steep incline is more difficult to irrigate thoroughly than is more level land. The influence of drouth induced by these practices and circumstances on the production of bottleneck and related malformed potatoes was studied and observed.

Malformed tubers resulting from delaying the first irrigation.

An exploratory experiment was performed in 1946 in two commercial fields of potatoes by withholding irrigation water during early tuber development. In one case the potatoes were planted May 15 on land that had produced potatoes the two previous cropping years, and the first irrigation (July 9) was withheld from four plots. At this time the largest tubers were ½-inch to 1-inch in diameter. The second irrigation (July 19) was applied to these plots, and they received all subsequent irrigations. At the time of the July 19 irrigation, the plants in the dry plots were dark green in color in contrast to those irrigated July 9. The second field of potatoes was planted June 4 in freshly plowed

alfalfa land. One irrigation was applied to this field of young potato plants July 13 before tuberization started. The following two irrigations, July 23 and 30, were withheld from four plots, and when irrigated again, August 6 and 7, these plots were dark green in color in contrast to those receiving all irrigations. When irrigations were resumed the largest tubers in the dry plots were 1-inch to 1½-inches in diameter. The highly water-absorptive alfalfa land dried out slowly during this, the warmest part of the growing season.

After harvest the tubers were examined for malformed types, and an analysis of the data showed that the drouth treatment during early tuber growth increased the yield of bottleneck tubers. The dumbbell and pointed-bud-end tubers were more numerous, but the increase was not significant. The drouth treatment did not alter the total yield, but the yield of U. S. No. 1 grade was reduced.

A similar experiment was performed in 1947. The potatoes were planted in moist soil May 10. This spring was comparatively warm and all plots were given a light irrigation July 2, when the plants were 8 to 10 inches high. The control treatment received all subsequent irrigations. One set of four plots received no irrigation July 13 or 19 and irrigations were resumed July 28. Water was withheld from a second group of plots July 28 and August 4, and again supplied August 13. Both sets of drouth treated plots were dark green when irrigation was resumed.

The harvested tubers were examined and placed in that malformed group they most closely resembled. The data are summarized in Table 1.

The earlier drouth period (July 13 and July 19) reduced the number of normal tubers and increased the total number of malformed tubers. Of the several malformed types only the twisted tubers were significantly more numerous as a result of the earlier drouth treatment; however, the same population trends are evident for the bottleneck and pointed-bud-end tubers. Since the early drouth treatment increased or tended to increase the number of tubers in each malformed category, this response indicates that the several malformed types are related with respect to causation. These data further suggest that the plant and tuber size at the time of drouth influences the number and type of malformed tubers produced.

Malformed tubers resulting from varying the planting date.

The date of planting potatoes in eastern Idaho may vary from late April until mid-June. Potato irrigation for much of the Upper Snake River valley starts in late June or early July. By the time of the first irrigation potatoes planted in late April or early May are generally in early bloom and many plants are developing tubers. That drouth frequently limits plant growth is

indicated by the rapid vegetative growth and the lighter green foliage that develops two or three days after the first irrigation.

Table 1. Relative yield of malformed tubers by potato plants subjected to drouth at two periods of tuber growth.

Irrigations withheld	Average number of tubers per plot							
	Total	Normal	Bottle-neck	Dumb-bell	Pointed-bud-end	Twisted	Total malformed	Percent normal
None after July 2	140.3	94.5	13.5	6.5	12.2	13.5	45.7	67.3
July 13 and 19	137.7	62.3	25.7	8.2	22.0	19.5	75.5	45.2
July 28 and Aug. 4	144.5	88.3	11.5	10.0	19.5	15.2	56.0	61.1
L. S. D. 5 percent	N.S.	26.7	N.S.	N.S.	N.S.	5.7	18.1	

The influence of planting date on the production of malformed tubers was demonstrated by an experiment in 1947. The first planting was made April 28 and at 10-day intervals additional plantings were made by hand until five plantings were completed on June 7. All plots received the first irrigation July 2 and the same irrigation schedule for the remainder of the season. Following harvest, the number of bottleneck and dumbbell tubers were counted and compared with the total number of potatoes produced in each plot. The yield of commercial grades was also determined. The data are summarized in Table 2.

The number of malformed tubers produced was correlated with the age of the plants or their planting date. The earliest planted potatoes produced the largest number of malformed tubers. The data indicate that bottleneck potatoes are produced by smaller tubers than are dumbbell potatoes. Very few dumbbell potatoes were produced by plants from the last two planting dates. For these same plots there were considerably more bottlenecks even though the differences are not significant.

The number of malformed potatoes produced is correlated with the yield of U. S. No. 2 grade for the several planting dates. The yield of No. 2 grade is inversely related to the yield of U. S. No. 1 grade while the total yield of potatoes was the same for all planting dates. The bottleneck and dumbbell tubers do not account for all the potatoes placed in the No. 2 grade. The other malformed types, i.e., twisted, pointed-bud-end and knobby, also contributed to this grade. It is evident however, that the yield of No. 2 grade closely parallels the number of bottleneck and dumbbell potatoes produced, and that a large number of these malformed potatoes reduces the number and weight of normal potatoes (U. S. No. 1. See also Table 1). The relationship of early planting with poor commercial quality of the harvested crop has been demonstrated experimentally and commercially for a number of years and has discouraged the use of early planting where surface irrigation is practiced.

Table 2. The influence of planting date on the yield of malformed tubers and commercial grades of Russet Burbank potatoes. All potatoes received the first irrigation July 2, 1947.

Planting date	Average number of tubers per plot				Average yield per plot—pounds			
	Bottle-neck	Dumb-bell	Total malformed	Total tubers	U.S. No. 1	U.S. No. 2	Total	Percent U.S. No. 1
April 28	24.0	21.2	45.2	136.3	17.3	26.1	56.2	30.7
May 8	10.0	8.0	18.0	138.3	28.8	17.4	54.0	53.5
May 18	8.2	.5	8.5	142.0	34.6	14.5	55.7	62.1
May 28	3.5	.5	4.0	145.8	34.7	7.1	48.3	71.8
June 7	1.2	.2	1.5	136.3	29.2	5.8	43.5	67.1
L. S. D. 5 percent	10.0	5.6	12.5	N.S.	8.4	8.1	N.S.	

Preceding experiments demonstrate that drouth caused by withholding early irrigation water, or planting potatoes early with no advance of the initial irrigation date will increase the production of malformed potatoes. For the 1948 growing season an experiment was designed to simultaneously test the influence of both factors on the production of malformed tubers. A split-plot design was used and the plots were randomized in each of seven blocks and planted on the following dates: 4-22, 5-1, 5-14, 5-29 and 6-12. One-half of each split-plot received the first irrigation June 3, and succeeding irrigation on 6-16, 7-5 and 7-11. On July 11, the second half of each split-plot was irrigated. All plots received the same irrigation treatment for the remainder of the growing season. The data from this experiment are summarized in Table 3.

The causative relationship of drouth during early tuber

Table 3. The effect of date of planting and time of first irrigation on the yield of malformed tubers in the Russet Burbank variety. Data from a split-plot experiment, 1948.

	Average yield of malformed tubers per plot—pounds				Average yield of commercial grades per plot—pounds			
	Bottle-neck	Dumb-bell	Pointed-bud-end	Total malf'md	U. S. No. 1	U.S./a No. 2	Total	Percent U.S. No. 1
			Influence of Planting Date					
April 22	18.8	3.0	3.5	25.4	119.9	3.4	178.9	67.0
May 1	16.1	2.9	3.5	22.6	123.8	1.9	182.6	67.8
May 14	10.4	1.1	3.8	15.3	136.8	2.2	190.5	71.8
May 29	0.3	0.1	0.4	0.8	140.6	3.8	184.3	76.3
June 12	0.04	0.05	0.0	0.1	91.3	0.5	139.9	65.3
L. S. D. 5%	7.4	1.4	2.6	9.0	22.2	N.S./b	24.6	
			Influence of date of first irrigation					
June 3	1.8	0.8	0.4	3.0	124.0	0.7	168.2	73.7
July 11	16.4	2.2	4.1	22.7	121.0	4.0	182.3	66.4
L. S. D. 5%	4.2	1.0	2.1	4.2	N.S./b	2.6	N.S./b	

/a Weight of No. 2 grade potatoes remaining after the bottleneck, dumbbell and pointed-bud-end tubers had been removed.
/b N.S. means not significant.

growth to the development of malformed tubers of the bottleneck and related types is clearly shown by these data. Advancing the irrigation schedule about 1 month greatly reduced the yield of malformed tubers for early planted potatoes, and correspondingly increased the percentage of U. S. No. 1 grade. As in the previous experiment the bottleneck tubers were most numerous of the malformed types and the data again suggest that they develop from smaller tubers than do the dumbbell or pointed-bud-end types. It is again evident that the three malformed-tuber types are related in that they develop on plants predisposed by the same factor. It is also evident from the weights of U. S. No. 2 grade in Table 3 that the workmen placed in this grade other malformed tubers that developed as a result of the irrigation treatment.

The elapse of time between planting and the initiation of irrigation appears to be an important relationship in preventing the velopment of bottleneck and related tuber types when Russet Burbank is grown under irrigation. In the preceding experiment (Table 3) the interaction, date of initial irrigation x planting date, was significant for the several categories of malformed

Table 4. Differences in yield of malformed tubers due to starting the irrigation schedule June 3 and July 11 for several dates of planting.

Planting date	Average yield in pounds per plot			
	Bottleneck	Dumbbell	Pointed-bud-end	Total
April 22	27.7	2.7	5.5	37.0
May 1	28.1	3.0	6.2	37.4
May 14	16.8	1.6	6.1	24.4
May 29	0.4	-0.1	0.7	0.9
June 12	-0.1	-0.1	0.0	-0.1
L. S. D. 5%*	10.3	1.7	3.7	11.4

* The differences in each column are significant at the 5 percent level if they equal the L. S. D. values given.

tubers. Most of the malformed tubers were produced by the plants initially irrigated July 11. The difference in yield of malformed tubers for the plots irrigated June 3 and July 11 was large for the early planted potatoes; however, there was no difference for the last 2 planting dates (Table 4). In this experiment those potatoes planted 43 days (May 29) or less prior to the initial irrigation had a minimum of malformed tubers.

This relationship was further studied by using data from Tables 2 and 3 and from other experiments not reported to compute a correlation coefficient between the yield of U. S. No. 1's (percentage) and the number of days between planting and the first irrigation. Twenty-two pairs of data were used for this analysis and a correlation (r) of -.6004 was computed. This value is significant and confirms the premise that the Russet Burbank variety will yield a greater proportion of normal tubers

if the irrigation schedule is advanced toward the planting date. On the basis of information now available, malformed tubers of the bottleneck and related types will be at a minimum if the irrigation program is started 30 to 40 days after planting.

Slope of land as a factor in producing malformed potatoes.

One of the fields used for plot work in 1946 had a perceptible slope near one end. The irrigation water ran rapidly over this area and soaked the soil poorly unless small streams were used and allowed to run for considerable time. The block arrangement of plots was such that two blocks traversed the slope, one block was on fairly level land above the slope and the fourth on level land below. The whole field produced bottleneck tubers due to an inadequate first irrigation, but the plots located on the slope were severely affected. Some plots on the slope produced only 4 to 5 percent normal tubers. When the potatoes from these plots were graded, only commercial grades were recorded. The yield of U. S. No. 2's reflects the relative production of bottle-

Table 5. The effect of a slope in the land on the yield of malformed tubers. Malformed tubers represented as U. S. No. 2 grade.

Block No.	Location of block with respect to slope	Average yield in lbs. per plot U. S. No. 2
1	Level land above slope	24.8
2	Incline, comprising roughly upper half	
2	Incline, comprising roughly upper half of slope	32.5
3	Incline, lower half of slope	36.2
4	Slight incline, delta-like below slope	28.4

neck and related tuber types as this grade was comprised almost entirely of these malformed tubers (Table 5). Potatoes severely malformed were discarded as cullage, thus actually minimizing the extremes that existed.

The effect of defoliation on the production of malformed tubers.

Summer hail storms occasionally mutilate the foliage of potato fields. One grower reported that most of the foliage in one of his fields was destroyed in late July. The plants recovered, but the crop of potatoes was mainly No. 2 grade because of numerous bottleneck tubers. The relationship of defoliation to the development of malformed tubers was tested by pruning rapidly growing plants after tuberization had started.

In an exploratory experiment, Russet Burbank plants growing in rows across a greenhouse bench were pruned from 18 inches to 10 inches when they were in the late bud and early bloom stage of growth. Several weeks elapsed before new growth

was approximately equal to the original vine growth. The potatoes were harvested about 7 weeks after pruning and the types of malformed tubers produced noted. Pruning reduced the size of tubers and altered their shape. The relative numbers of normal and malformed tubers produced by the pruned and non-pruned plants were: normal, 17 and 36; malformed, 27 and 14, respectively. The malformed tubers were of the bottleneck and related types.

Under field conditions, replicated plots of potato plants were pruned back about 8 inches on August 3, 1946. When the potatoes were examined following harvest the workmen did not observe that the pruning treatment had reduced tuber size, and the numbers of normal and malformed tubers were not counted. The only data recorded were the relative weights (in pounds) of malformed and normal tubers produced. Since the pruning treatment altered both the weight of potatoes produced and their morphology, it was impossible to separate the morphological changes from the weight data. Consequently, the data were summarized by computing the averages and are presented in Table 6.

A greater proportion of the tubers from the pruned plants were malformed than were those from the non-pruned plants. The relative yield of knobby potatoes (Table 6) as a result of the pruning treatment indicates that in the Russet Burbank variety this malformation is caused by factors different from those responsible for secondary tuber elongation.

Circumstantial evidence was obtained in 1947 supporting the observation that defoliation of Russet Burbank plants by natural means will predispose tubers of such plants to develop into malformed types. In the Egin Bench area, west of St. Anthony, sub-irrigation is used almost exclusively for crop production. This method of irrigation maintains a uniform supply of water to the growing crop. In general, potatoes produced in this area have better conformation to Russet Burbank type than those from any other section of Idaho. In 1947, potatoes in this area were planted in late April and early May. By late June, the plants were developing flower buds; and on June 29 and 30 killing frosts destroyed much of the foliage. New vines developed and a crop of potatoes was harvested but the harvested crop contained an unusual number of bottleneck tubers. The shipments from a single packing shed show that five railroad carloads of U. S. No. 2's were shipped from the 1946 crop and 25 carloads from the 1947 crop.[1]

At Murtaugh, Idaho, a crop of potatoes was planted about May 1, 1947. At this more southerly location and lower elevation

[1] This information was supplied by Mr. Rex L. Blodgett, Director, Research and Service, Idaho Potato Growers, Inc., Idaho Falls, Idaho, and confirmed by the following communication from Mr. Floyd R. Broadhead, formerly County Extension Agent, St. Anthony, Idaho. " . . . . . Approximately 25 to 30 percent of the tubers (were) affected by a bottleneck malformation in the harvested crop. This was an increase in bottleneck tubers of 20 to 25 (percent) over 1946. In 1946, there was very little, if any, bottleneck tuber production . . . . . ".

Table 6. The effect of pruning potato plants on the production of malformed tubers. Potato plants pruned back about 8 inches August 3, 1946. The figures in the table are the average of 4 plots.

Treatment	Average yield in pounds per plot				
	Normal	Bottleneck	Pointed bud-end	Knobby	Total
Pruned	23.3	15.4	7.8	0.7	47.2
Not pruned	59.4	9.9	2.8	4.3	76.5

the potatoes were in bloom at the time of killing frosts on June 29 and 30. Here again much of the foliage was destroyed but the vines recovered and produced a crop of potatoes. It is estimated that 50 to 60 percent of the harvested potatoes were typical dumbbell tubers.[2]

These qualitative data and the circumstantial evidence support the observation that partial defoliation of plants during early tuber growth will induce the development of malformed tubers. Since the defoliated plants produce tubers having the same malformations as those subjected to drouth in the earlier experiments, the two treatments apparently have the same effect on small tubers. Gilbert et al., interpret the drouth effect as checking tuber growth and causing them to mature. A later supply of water induces renewed growth in the partially matured tubers (5). Defoliation would similarly arrest tuber growth and possibly cause maturation. As soon as the destroyed vines were regenerated, the plant could then support renewed tuber growth. In the Russet Burbank variety the renewed (secondary) tuber growth following drouth or defoliation produces tubers of the bottleneck and related malformed types.

Specific gravity differences between stem- and bud-ends of malformed tubers.

It has been reported that tubers affected with second growth have a low specific gravity. When using salt solutions for measuring specific gravity of Russet Burbank tubers, it is evident that the stem-end of bottleneck tubers has a lower specific gravity than the bud-end as the tuber assumes a vertical position in the solution with the stem-end projecting toward the surface. Specific gravity measurements were made of the stem- and bud-ends of the several tuber forms illustrated in Figure 1 to see how these specific gravity values differed from normal tubers. The potatoes for the experiment were selected from a badly deformed crop that suffered drouth during early tuber growth. Normal tubers were also selected from this crop of potatoes and from a crop having few malformed tubers. Each of the four malformed types as well as the normal tubers was represented by six tubers weighing 2 to 4, 4 to 6, 6 to 8 — and 12 to 14 ounces in weight. Salt solutions were used to measure the

[2] Loc. cit. R. L. Blodgett.

specific gravity of the stem- and bud-ends of all tubers. The tubers were cut in two as follows: bottlenecks, the bottleneck was severed from the bulbous bud-end; dumbbell, the tubers were cut at the constriction; twisted, cut at the region of greatest curvature; pointed-bud-end, the distal outgrowth from the larger stem-end. The normal tubers were cut in half approximately at the center of the longitudinal axis. The differences in specific gravity between the 2 ends of the malformed tubers are summarized in Table 7.

The specific gravity of the respective ends of the potatoes varied with the type of malformed tuber. For the bottleneck and twisted tubers the stem-ends had a lower specific gravity than the bud-ends. The reverse was true for the pointed-bud-end tubers. The stem-ends of normal tubers not subjected to drouth had a higher specific gravity than the distal-ends. This relationship was reversed for the normal tubers taken from the crop subjected to drouth during early growth. Although the difference in specific gravity of the two ends in this latter case was not significant, it appears that physiological changes occurred in these morphologically normal tubers similar to the changes in the bottleneck and twisted types.

Table 7. Specific gravity values for stem- and bud-ends of malformed and normal Russet Burbank tubers.

Tuber type	Stem-end	Bud-end	Difference
Bottleneck	1.0657	1.0782	-.0125
Dumbbell	1.0757	1.0746	+.0011
Twisted	1.0707	1.0775	-.0068
Pointed-bud-end	1.0807	1.0714	+.0093
Normal[1]	1.0790	1.0811	-.0021
Normal[2]	1.0709	1.0811	-.0021
L. S. D. 5 percent			.0032*

[1] Normal tubers from adjoining field. This field of potatoes did not suffer from drouth.
[2] Normal tubers from same field as malformed tubers.
* Differences are significant if they equal or exceed this value.

Jelly-end rot in malformed tubers.

Jelly-end rot is a peculiar decay long associated with the Russet Burbank and Burbank varieties grown in Idaho and other western states. On the basis of observations made in this study, jelly-end rot always occurs at the stem-end of the affected tuber. The rot may be present at harvest time or develop later in storage. It is associated with malformed tubers of the bottleneck and related types.

An affected tuber when taken from the soil will be very soft to the touch at the stem-end. The rotted portion is fragile and easily broken in handling (Fig. 4). The rot has a jelly-like consistency devoid of any fibrous texture and very watery. Its color may vary from almost colorless, through straw to increasingly darker shades of brown. In appearance this rot is similar to the watery, jelly-like decay that ultimately destroys many exhausted seed pieces.

Figure 4. Bottleneck tubers with jelly-end rot. These tubers had shrivelled stem-ends when placed in moist chamber and the rot developed in a 14-day period.

Jelly-end rot does not destroy the entire tuber, and rarely destroys more than 1 to 2 inches of stem-end tissue of malformed tubers.[3] The demarcation between rotted and healthy tissue is sharp. Under storage conditions the water from the rot soon evaporates leaving a shrivelled clump of epidermal tissue collapsed at the stem-end. When graded for commercial sale the tissues destroyed by the rot are cut from the tuber and the healthy portion graded as U. S. No. 2, if the healthy portion is large enough.

The etiology of jelly-end rot is not satisfactorily understood, and it was not the purpose of this study to investigate the problem.

[3] Some growers who have had many years' experience with the Russet Burbank variety claim to have observed tubers of normal conformation with jelly-end rot. Since normal appearing tubers from crops bady affected with bottle-neck type malformation tend to have a low specific gravity at the stem-end (Table 7), jelly-end rot may occur in "normal" tubers. The reasons for this interpretation will become evident later in this section.

Since the rot is associated with tubers having the bottleneck type of malformation, an opportunity arose to observe an ecological factor that might favor development of the disease in the field and storage. Preliminary laboratory studies testing this observation led to hypotheses concerning tuber susceptibility and the etiology of the rot. These observations and preliminary studies are briefly presented that they might be helpful to those seeking an understanding of jelly-end rot.

During the fall of 1946, after the killing frosts had destroyed all potato vines, irrigation water leaked from a ditch and ran down several rows of a potato crop containing many bottleneck tubers. The water ran unnoticed for some time as the soil was thoroughly wetted throughout the ridges covering the potatoes. When harvested several days later, jelly-end rot was prevalent in the bottleneck tubers harvested from the irrigated rows, but negligible in the bottleneck tubers from the dry contiguous rows. This observation suggested that abundant moisture is necessary for the development of jelly-end rot in bottleneck potatoes.

On October 3, 1947, 43 freshly harvested bottleneck tubers were taken to the laboratory, wetted and placed in six glass moist chambers. The tubers were supported on wire hardware cloth over about $\frac{1}{4}$ inch of water. Wetted cheese cloth was placed over the potatoes in each chamber and the cloth edges forced into the free water below. The cheese cloth served as a wick and kept the tubers wet. Forty-three additional bottleneck tubers were washed and placed in an open wooden box (about 10 inches high). Both lots of tubers were left in the unheated laboratory and the temperatures were generally in the high 50's and 60's° F. The potatoes were examined for jelly-end rot October 22. Fifteen of those kept moist had typical jelly-end rot, while seven of those in the open box had the rot. Glass slide smears were prepared from the rotted tissue from some of the tubers and two morphological types of bacteria were evident upon microscopic examination. The jelly-like tissue from 15 tubers was used for preparing water suspensions and dilution plates were poured using nutrient agar as the medium. Tissue plantings from the same decaying tubers were also made to solidified potato-dextrose-agar. Fifteen days later, bacteria had grown in the dilution plates prepared from 9 of the tubers, and the plates from 6 remained free of organisms. Four fungi in addition to bacteria grew from the tissue plantings.

On October 23, 1947, a second laboratory test was started. The bottleneck tubers were similar to those used in the first test having been harvested from the same field October 3. They were washed after harvest and held until October 23 in open wooden boxes in an unheated room. By this time the stem-ends of some bottleneck tubers were soft and shrivelling (Fig. 2). Twenty-one of the potatoes having the soft and shrivelled stem-ends were placed in three glass moist chambers as described above, and a similar number of bottleneck tubers having firm stem-end were

likewise treated. In addition, 21 normal tubers harvested October 5 and held in the storage cellar until the time of the test were also placed in glass moist chambers. The 3 sets of tubers were examined for jelly-end rot November 6. Fourteen of the bottleneck tubers having shrivelled stem-ends developed typical jelly-end rot (Fig. 4), and none of the bottleneck tubers with firm stem-ends or the normal tubers developed the decay. Water suspensions were prepared from the 14 jelly-end rot tubers on November 7 and dilution plates poured. Bacteria grew in the plates prepared from four of the tubers, a fungus from one, and no growth developed in the plates from nine tubers.

In late October, 1947, 16 tubers with jelly-end rot were collected from the storage cellar and isolations made from them by the dilution plate method. On November 6, bacteria had grown in the plates from seven diseased tubers; a fungus was growing in the plates with the bacteria from one tuber; and the plates from nine tubers remained free of organisms. Owing to the limited time available, the senior author did not critically examine or evaluate the pathogenicity of any of the organisms isolated.

These observations and preliminary studies prompt the tentative conclusions that jelly-end rot of Russet Burbank potatoes is a disease confined to tubers that have undergone secondary growth. Malformed tubers that shrivel at the stem-end are particularly susceptible, and these tubers are deficient of starch in the stem-end. An abundance of moisture favors the development of the rot.

The number of isolations in which organisms failed to grow suggests that jelly-end rot may be a physiological breakdown of tissues depleted of starch and other components. If an organism causes the rot, it is a weak pathogen as its activities are confined to tissues largely exhausted of the storage products that are normally used by plant tissues to form barriers of resistance to invading pathogens. Irrigation or other practices that eliminate secondary tuber growth and the resultant glassy-end potatoes will probably control jelly-end rot.

Discussion

It is believed that the drouth conditions induced by withholding the initial irrigation or planting early without advancing the irrigation schedule was not seriously influenced by natural precipitation. The average precipitation for the months of May and June over a 37-year period at Aberdeen, is 1.83 inches. In 1947 a total of 2.3 inches of rain fell between the first planting date, April 28 and the initial irrigation, July 2. On 3 days during this period there was an excess of .50 of an inch of rain, i. e., May 11, .74 of an inch; June 8, .68; and June 11, .53. The remaining rain came in 8 showers with the heaviest precipitation contributing .17 of an inch on June 2. In 1948 there was a total precipita-

tion of 2.55 inches between the first planting, April 22 and the delayed first irrigation of July 11. In one storm on June 22, .80 fell, and the remaining precipitation came in 13 showers with the heaviest precipitation from a single storm amounting to .35 of an inch. The water from any one rain storm in the springs of 1947 and 1948 would have penetrated the soil a few inches at most and would have benefited a growing crop for a relatively short time.

The plants subjected to these drouth treatments did not wilt. At the time of the first irrigation the larger plants were small for their age. They were dark green in color with the leaflets undersize and rigid. The whole plant appeared "hard" and stood erect. Following irrigation the new vine growth was rapid, light green in color and succulent.

The starch-free tissue in the stem-ends of malformed tubers and the association of this glassy tissue to jelly-end rot provokes interest as to its origin. Penman (12) presents two hypotheses to explain the development of the starch free tissue. The first explanation is based on a change in the physiology of small immature tubers at a time when little dry matter is elaborated, and the equilibria between dextrose, sucrose and starch have in some way been shifted toward the sugar side leaving the glassy tissue rich in sugars. The second explanation and the one he believes more probable assumes that the small tubers were normal with starch stored in all internal tissues. A stimulus associated with renewed vine and tuber growth causes the starch to be hydrolyzed to the soluble sugars and the latter are translocated from the stem-ends. This explanation is supported by chemical analytical data that show a striking difference in the starch-sugar relationship of glassy and normal tuber storage tissue. Penman suggests that after the limiting factor drouth is removed, the plants may be unable to synthesize sufficient carbohydrates for the renewed growth and the starch in stem-ends of tubers is digested to sugars and translocated into the plant system.

This explanation seems more tenable in accounting for the glassiness observed in tubers in this study. The vigorous vegetative growth following the initial irrigations was pronounced and may have required additional carbohydrates and other synthesized products that were supplied from the stem-ends of young tubers. The hydrolysis of starch and the translocation of carbohydrates from a seed piece suggest that the carbohydrates from the glassy tissue were utilized in the growth of the plant. In the seed piece the starch is first hydrolyzed in proximity of the bud that produces the new plant. By analogy, the starch in proximity of the stolon connection (stem-end) of the young tuber is hydrolyzed and translocated through the stolon to the mother plant. After the starch and other storage products of a seed piece have been utilized in producing a plant, the synthetic products from the new vegetatively mature plant are not translocated to the tissues of the old seed piece. The seed piece remains

glassy and frequently develops a jelly-like rot. A similar relationship may prevail in the case of the glassy stem-end tissue. After the plant has attained a certain stature of vegetative growth, synthetic products are again translocated to the tubers or to form new tubers. Second growth (elongation) develops in tubers that had their growth arrested. The renewed growth proceeds from the distal end of the tuber and the carbohydrates translocated to the tuber are deposited as starch in the second growth and not in the depleted stem-end tissue.

The long-tuber varieties are apparently more susceptible to second growth than round-tuber varieties. The round-tuber varieties Sebago, Pontiac, Menominee, Charles Downing and others were grown in variety experiments with the long-tuber varieties Russet Burbank, Burbank, White Rose and Wurst Kartoffel. In a number of cases the long-tuber varieties produced many bottleneck tubers and jelly-end rot and no tubers of the round varieties were affected. Various family lines, selections and breeding stocks that possess the long-tuber type have been observed to be affected with second growth and jelly-end rot while similar potato material possessing round tubers was not affected.

Summary

Under irrigation the Russet Burbank variety of potatoes frequently produces numerous tubers malformed due to secondary growth or elongation. In this study the various forms assumed by the malformed tubers exhibiting secondary growth were designated bottleneck, dumbbell, twisted and pointed-bud-end. The yield of these tuber types was increased when the plants were retarded in their growth while the tubers were relatively small. Drouth is probably the most general causative factor; however, foliage destruction by hail, frost or mechanically after tubers have set will also increase the production of malformed tuber types. Drouth during early tuber growth was accomplished by withholding the first irrigation or planting early without advancing the irrigation schedule. In either case the growth of plants was retarded as evidenced by their small size, dark green color and erect habit of growth. A greater proportion of Russet Burbank tubers develop second growth, and the malformation of tubers is more serious if growth is retarded while the tubers are relatively small. Drouth or defoliation when the vegetative plant is in early bloom will cause many more bottleneck and similar tubers to form than the same treatments will when the plants are 2 to 3 weeks past the blooming stage. For most of eastern and southern Idaho drouth during late June and early July will cause much more second growth than a drouth in late July or August. On the basis of present information most of the bottlenecks, dumbbells, etc., can be eliminated by starting the irrigation schedule 30 to 40 days after planting.

The data indicate that bottleneck potatoes develop when the

growth of small tubers or young plants is retarded, and that dumbbells, twisted and pointed-bud-end tubers develop when the growth of larger tubers or plants is retarded.

The stem-ends of bottleneck and twisted tubers have a lower specific gravity than normal potatoes. Frequently, the stem-ends of these types and occasionally dumbbells shrivel in storage and the internal tissue is free of starch as evidenced by its glassy appearance and reaction to an I-KI solution. Jelly-end rot develops in these second growth tubers, particularly the bottleneck type in which the stem-end is partially or completely depleted of starch.

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